

Climbing, Brachiation, and Terrestrial Quadrupedalism: Historical Precursors of Hominid Bipedalism

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ABSTRACT The vertical-climbing account of the evolution of locomotor behavior and morphology in hominid ancestry is reexamined in light of recent behavioral, anatomical, and paleontological findings and a more firmly established phylogeny for the living apes. The behavioral record shows that African apes, when arboreal, are good vertical climbers, and that locomotion during traveling best separates the living apes into brachiators (gibbons), scrambling/climbing/brachiators (orangutans), and terrestrial quadrupeds (gorillas and chimpanzees). The paleontological record documents frequent climbing as an ancestral catarrhine ability, while a reassessment of the morphology of the torso and forelimb in living apes and Atelini suggests that their shared unique morphological pattern is best explained by brachiation and forelimb suspensory positional behavior. Further, evidence from the hand and foot points to a terrestrial quadrupedal phase in hominoid evolution prior to the adoption of bipedalism. The evolution of positional behavior from early hominoids to hominids appears to have begun with an arboreal quadrupedal-climbing phase and proceeded through an orthograde, brachiating, forelimb-suspensory phase, which was in turn followed by arboreal and terrestrial quadrupedal phases prior to the advent of hominid bipedality. The thesis that protohominids climbed down from the trees to become terrestrial bipeds needs to be reexamined in light of a potentially long history of terrestriality in the ancestral protohominid. © 1996 Wiley-Liss, Inc.

If "missing links" are to be tracked with complete success, the foot, far more than the skull, or the teeth, or the shins, will mark them as Monkey or as Man . . . It is in the grades of evolution of the foot that the stages of the missing link will be most plainly presented to the future paleontologist . . . (From *Arboreal Man* by F. Wood Jones, 1916, p. 73.)

The origin of human bipedalism is one of paleoanthropology's most persistent mysteries. The problem, as recognized early on, is how to explain the evolutionary transformation from an ancestral arboreal ape to a terrestrial, upright bipedal hominid. The morphological changes associated with this transformation, especially in the lower limb, are unique and extreme, and yet we know that this evolutionary event occurred. How

do we explain the ape-to-hominid transformation?

In 1923, Sir Arthur Keith postulated four sequential phases in human evolution: a pronograde catarrhine monkey-like ancestor, a small-bodied, orthograde, brachiating gibbon-like ancestor (the hylobatians), a large-bodied, orthograde, arboreal ape ancestor (the troglodytians), and a hominid phase of plantigrade progression (i.e., bipedalism) on the ground (Keith, 1923). In Keith's view, brachiation and arm suspension explained many of the morphological features of the

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upper limb and thorax shared by living apes and humans. Keith's troglodytians, which supposedly preceded hominid bipedalists, practiced frequent brachiation. Widely adopted at first, Keith's "brachiationist" hypothesis fell into disfavor in the following decades, with even Keith (1940) abandoning his own explanation (see Tuttle, 1974, for an excellent review). It was not until the 1970's that a single perspective would again take precedence over alternative views.

In 1971 and 1975, Stern synthesized a host of information concerning primate locomotion and postulated that "the human ancestor was predominately adapted for life in the trees, employing its forelimbs much as does the living orangutan, and its hindlimbs in a somewhat more pronograde quadrupedal manner" (1975, p. 59). Thus was born what is now known as the "vertical-climbing hypothesis," which suggests that climbing is the "biomechanical link between brachiation and bipedalism" (Fleagle et al., 1981, p. 359). The vertical-climbing hypothesis not only gives an alternative explanation for the shared ape-human upper limb and thorax morphology, replacing the brachiation hypothesis championed by Keith (1903, 1923), Gregory (1916, 1927a,b, 1928 a,b), Morton (1924b), and others, but also posits vertical climbing as the critical positional behavior preadaptive for hominid bipedality. Today, the vertical-climbing hypothesis is the most generally accepted view, and other explanations (i.e., brachiation, suspensory, quadrupedal, or knuckle-walking models: Straus, 1949, 1962; Hooton, 1946; Avis, 1962; Washburn, 1963, 1968a,b, 1971; Lewis, 1969, 1989; Simons and Pilbeam, 1972; Tuttle, 1974; Corruccini and Ciochon, 1976; Corruccini, 1978; Zihlman, 1979, 1984; Sarmiento, 1988; Hunt, 1991a,b; Gebo, 1992a; Begun, 1994) are given a less favorable reception.

In this report, I examine a variety of evidence that suggests that vertical climbing is not sufficient to explain the ape/human body form, and does not represent the critical locomotor behavior preceding bipedalism. Four specific questions will focus our attention on particular aspects of the behavioral and anatomical record that I believe require some rethinking. First, how frequent is climbing in general and vertical climbing in particular

in the locomotor behavior of primates? Second, what behaviors have shaped the upper body and forelimb anatomy of living apes? Third, what type of a body plan did the ancestral protohominid possess? Fourth, which historical explanation best interprets the sequence of evolutionary locomotor events leading up to the appearance of hominid bipedalism?

THE VERTICAL-CLIMBING HYPOTHESIS

In his landmark works of 1971 and 1975, Stern argued on the basis of hip and thigh musculature that the human condition most resembled that of atelines, particularly *Alouatta*, with a few resemblances to *Pongo* and *Hylobates*. He related this to the use of limbs in tension or what he called antipronograde behavior, which included climbing and forelimb and hindlimb suspensory movements and postures. Stern noted no special resemblances in the arrangement of hip musculature between African apes and humans. In Stern's reconstruction, the protohominid used its forelimbs as does the living orangutan. The only evidence which Stern considered that did not conform to his overall scheme of ape and human evolution were the similarities between human and African ape carpal bones (Lewis, 1972a-c; Jenkins and Fleagle, 1975). Stern (1975, pp. 67-68) further speculated that:

Long arms are likely to be evolved in an arboreal setting under circumstances which promote extensive use of the upper limbs in tensile activities. Such use would lead to a forelimb structure poorly suited for bearing the stresses of pronograde quadrupedalism. . . . Possibly the gorilla and chimpanzee were able to adjust to the stresses of quadrupedalism because their upper limbs were not too long nor so completely adapted to antipronograde activities as to preclude the reassumption of quadrupedalism. Possibly the upper limbs of man's ancestors were so long and so completely adapted to antipronograde activities that the only reasonable choice upon descent to the ground was to free them from locomotor function.

Stern and his colleagues continued to explore muscle function using electromyographic techniques (EMG) (Stern et al., 1977, 1980a,b; Vangor, 1977, 1979; Jungers and Stern, 1980), and this body of work led to the most explicit publication concerning

the vertical-climbing hypothesis, that of Fleagle et al. (1981). In this article, these authors argued that forelimb muscles in atelines and apes were more active during climbing and hoisting behaviors than during brachiation, and that bone strain tests on ulnae suggested that brachiation and climbing showed similar magnitudes of force. Further, the kinematic work of Prost (1980) showed that vertical climbing in chimpanzees was most similar to human bipedalism, as did Vangor's (1979) EMG work on ateline hindlimbs. On the other hand, little similarity could be shown to exist in hindlimb function between the bipedalism of primates and human bipedalism from the experimental techniques of EMG, kinematics, or force-plate studies (Elftman, 1944; Jenkins, 1972; Tuttle et al., 1979; Vangor, 1979; Kimura et al., 1979; Prost, 1980). Fleagle et al. (1981) further state that: "These studies suggest that many aspects of forelimb anatomy that have previously been identified as brachiating adaptations can be explained as well or better as adaptations to vertical climbing" (p. 361) and "Thus vertical climbing, more than any other locomotor activity, would appear to be functionally pre-adaptive for the type of hindlimb function seen in human bipedalism" (p. 371). Since 1981, several other publications have accepted this explanation (Aiello, 1981; Tuttle, 1981; Stern and Susman, 1982, 1983; Jungers and Stern, 1983; Susman et al., 1984; McHenry, 1984, 1991; Ishida et al., 1984, 1985; Tuttle et al., 1991a,b; Senut, 1991; Schmid, 1991; Rose, 1991; Heinrich et al., 1993; Duncan et al., 1994).

Cartmill and Milton (1977) examined wrist anatomy in lorises and galagos and found that lorises share a variety of anatomical features with that of the living apes (i.e., a non-articulating pisiform and ulna, a new ulnar head, and loss of ulnotriquetral contact). They suggest that since lorises, which are non-brachiating primates, share this suite of anatomical features with the living apes, these features need not be attributed to brachiation, and are more likely to have been associated in the ancestral great apes with slow and deliberate locomotion (e.g., climbing and bridging), contra Lewis (1972a-c, 1974). "It . . . seems likely," Cartmill

and Milton conclude, "that the great apes developed their "brachiating" adaptations directly from a cautiously-moving quadrupedal ancestor without going through a phase characterized by hylobatid-like bimanual suspensory behavior" (1977, p. 267).

Although Stern (1975), Cartmill and Milton (1977), and Fleagle et al. (1981) made primarily functional assessments, which were not intended to be phylogenetic hypotheses, the ideas contained within them do have implications for the sequence of events for ape and/or hominid evolution. The models emphasize climbing as an explanation for the ape body plan, and for Stern (1975) and Fleagle et al. (1981), the ancestral protohominid as well. The emphasis on arboreal locomotion and the lack of a phylogenetic context have two main implications for protohominid models. First, since African apes are only partly arboreal, their full behavioral repertoire is irrelevant to models that explain bipedalism; and second, the lack of an associated phylogeny obscures the intended sequence of adaptive events. For example, Stern's 1975 speculation that early hominids became bipedal because their arms were too long to permit a chimpanzee-like quadrupedalism (pp. 67-68) implies either that *Pongo* and hominids are sister taxa (Fig. 1A), a view not widely held today, or that long arms evolved in parallel three times among the hylobatid, the orangutan, and the hominid lineages (Fig. 1B), a very unparsimonious assumption. The most explicit phylogenetic assessment of ape and human locomotor evolution at this time was presented by Tuttle (1975), who likewise adhered to a climbing and suspensory model, excluding brachiation to explain the innovative upper limb and thorax characteristics of apes and humans. In his phylogenetic scheme (Fig. 1C), hominids are the sister taxon of all three great ape genera, a phylogenetic scheme not accepted today. Tuttle (1975) hypothesized pre-brachiating gibbons as best representing the prehominid condition, whereas Stern (1975) believed orangutans represented the best analog. In actuality, both views support an "orangutanian phase" or a highly arboreal movement pattern immediately prior to the adoption of hominid bipedalism. The phylogenetic implications of the vertical-

climbing model of Stern (1975) and others preclude an ancestral condition like that of African apes by selecting only the behavior climbing as being relevant to a prehomimid model (but see Washburn, 1968a,b; Zihlman, 1979, 1984). This interpretation is hampered by the now undoubted close phylogenetic association of African apes and humans as documented by modern molecular technology (e.g., Goodman et al., 1983; Sibley and Ahlquist, 1984; Ruwolo et al., 1991). The close relationship between African apes and humans, and the probable chimpanzee-human sister group in particular, implies, in contrast to the vertical-climbing models, that African ape terrestrial behavior and morphology may be extremely relevant for understanding the emergence of hominid bipedalism.

THE BEHAVIORAL RECORD

How often do living primates use general climbing and vertical climbing, and how do vertical climbing primates travel?

Two of the tenets of the vertical-climbing hypothesis are that 1) the climbing ancestor of all apes would have used this behavior frequently and 2) that the direct ancestor of hominids would have used it particularly often. Table 1 shows that few living primates use climbing, in the most general sense, more than any other type of locomotor behavior. The only primates that utilize climbing in an especially high frequency (i.e., greater than any other locomotor category) are gorillas and chimpanzees during arboreality, orangutans, gibbons during feeding, *Alouatta seniculus*, *Ateles* during feeding, and *Cercopithecus ascanius*. Frequencies for climbing are fairly high in a variety of species of Old World monkeys, although we do not normally think of these particular species as being "well adapted," especially osteologically, for climbing (i.e., cercopithecoids have dramatically reduced joint mobility throughout their limbs, Fleagle and Simons, 1982a; Gebo et al., 1988; Strasser, 1988; Harrison, 1989). Hunt (1991b) has even noted that baboons and chimpanzees vertically climb in a similar kinematic fashion.

Thus in an overall sense, chimpanzees and gorillas use climbing minimally, with the ex-

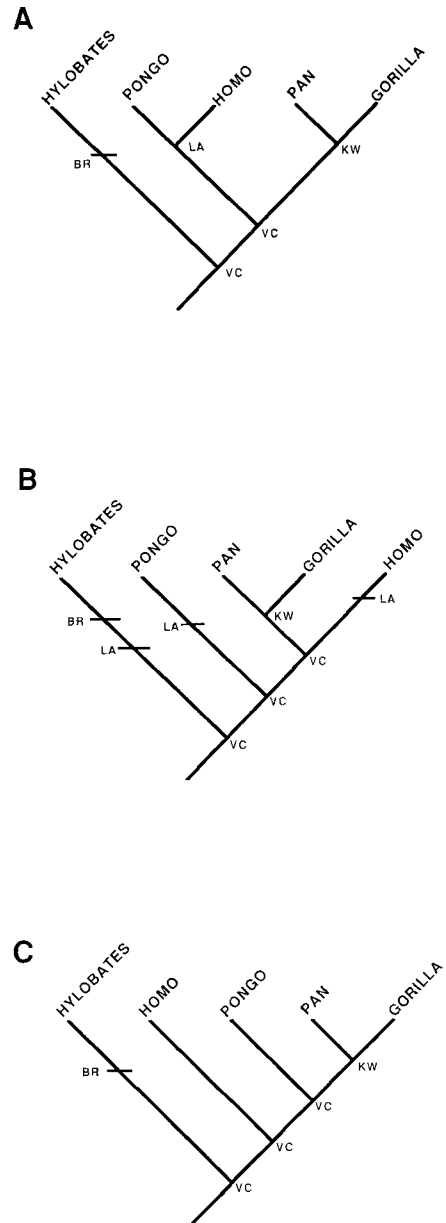


Fig. 1. Hominoid phylogenies. **A** and **B**, long arms have been mapped onto Stern's (1975) two potential phylogenetic views, while **C** reflects Tuttle's (1975) evolutionary assessment. VC, vertical climbing ancestral condition; BR, brachiation; KW, knuckle-walking; LA, long arms.

TABLE 1. Use of vertical climbing, generalized climbing, and brachiation in primates

	ACT ¹	VC (%) ²	CL (%) ³	LOCO (%) ⁴	BR% ⁵	Reference
<i>Gorilla gorilla</i>	All	<1	<1	Q 99	<1	Tuttle and Watts (1985)
<i>Gorilla gorilla</i>	Arboreal	56	78	Q 9	<1	Tuttle and Watts (1985)
<i>Pan troglodytes</i>	All	6	11	Q 86	1	Doran (1993b)
<i>Pan troglodytes</i>	All	5	5	Q 93	1	Hunt 1991
<i>Pan troglodytes</i>	Arboreal	56	69	Q 21	7	Doran (1993b)
<i>Pan troglodytes</i>	Arboreal	49	51	Q 37	5	Hunt (1991a,b)
<i>Pan paniscus</i>	All	?	31	Q 31	21	Susman (1984)
<i>Pan paniscus</i>	Arboreal	41	48	Q 23	17	Doran (1993a)
<i>Pongo pygmaeus</i>	Travel	18	69	Q 12	11	Cant (1987)
<i>Pongo pygmaeus</i>	Feed	33	77	Q 12	9	Cant (1987)
<i>Pongo pygmaeus</i>	Travel	10	53	BR 20	20	Sugardjito and van Hooff (1986)
<i>Hylobates syndactylous</i>	Travel	?	37	BR 51	51	Fleagle (1980a)
<i>Hylobates syndactylous</i>	Feed	?	74	BR 23	23	Fleagle (1980a)
<i>Hylobates lar</i>	Travel	?	21	BR 56	56	Fleagle (1980a)
<i>Hylobates lar</i>	Feed	?	51	BR 45	45	Fleagle (1980a)
<i>Hylobates pileatus</i>	Travel	6	6	BR 84	84	Srikosamatara (1984)
<i>Hylobates agilis</i>	Travel	?	14	BR 74	74	Gittins (1983)
<i>Hylobates agilis</i>	Travel	5	9	BR 48	48	Cannon and Leighton (1994)
<i>Alouatta palliata</i>	All	3	37	Q 47	—	Gebo (1992b)
<i>Alouatta palliata</i>	All	9	9	Q 70	—	Mendel (1976)
<i>Alouatta seniculus</i>	Feed	?	41	Q 59	—	Fleagle and Mittermeier (1980)
<i>Alouatta seniculus</i>	All	3	57	Q 33	—	Schön Ybarra and Schön (1987)
<i>Ateles geoffroyi</i>	Travel	16	29	Q 23	26	Mittermeier (1978)
<i>Ateles geoffroyi</i>	Feed	16	35	Q 25	28	Mittermeier (1978)
<i>Ateles geoffroyi</i>	All	7	16	Q 46	25	Cant (1986)
<i>Ateles paniscus</i>	Feed	?	45	BR 39	39	Fleagle and Mittermeier (1980)
<i>Ateles paniscus</i>	Travel	8	17	BR 39	39	Mittermeier (1978)
<i>Ateles paniscus</i>	Feed	10	36	BR 28	28	Mittermeier (1978)
<i>Chiropotes satanas</i>	All	2	30	Q 38	—	Walker (1993)
<i>Chiropotes satanas</i>	Feed	?	2	Q 88	—	Fleagle and Mittermeier (1980)
<i>Pithecia hirsuta</i>	All	?	11	Q 56	—	Happel (1982)
<i>Pithecia pithecia</i>	Travel	?	9	L 75	—	Oliveira et al., (1985)
<i>Pithecia pithecia</i>	All	2	29	L 41	—	Walker (1993)
<i>Cacajao calvus</i>	All	2	34	Q 36	—	Walker (1993)
<i>Cebus capucinus</i>	All	3	26	Q 54	—	Gebo (1992b)
<i>Cebus apella</i>	Feed	?	8	Q 88	—	Fleagle and Mittermeier (1980)
<i>Saimiri sciureus</i>	Feed	?	2	Q 87	—	Fleagle and Mittermeier (1980)
<i>Saimiri oerstedii</i>	All	?	5	Q 87	—	Boinski (1989)
<i>Saguinus mystax</i>	Travel	?	6	Q 56	—	Garber and Preutz (1995)
<i>Saguinus mystax</i>	Travel	?	11	Q 52	—	Garber and Preutz (1995)
<i>Saguinus midas</i>	Feed	?	2	Q 87	—	Fleagle and Mittermeier (1980)
<i>Saguinus oedipus</i>	Feed/forage	?	50	Q 26	—	Garber (1984)
<i>Saguinus fuscicollis</i>	Travel	?	12	Q 48	—	Garber (1991)
<i>Saguinus geoffroyi</i>	Travel	?	7	Q 43	—	Garber (1991)
<i>Saguinus mystax</i>	Travel	?	12	Q 52	—	Garber (1991)
<i>Cercopithecus ascanius</i>	All	1	43	Q 39	—	Gebo and Chapman (1995)
<i>Cercopithecus mitis</i>	All	1	35	Q 54	—	Gebo and Chapman (1995)
<i>Cercopithecus aethiops</i>	All	?	30	Q 54	—	Rose (1979)
<i>Cercocebus albigena</i>	All	5	35	Q 47	—	Gebo and Chapman (1995)
<i>Papio anubis</i>	All	1	1	Q 99	—	Hunt (1991b)
<i>Papio anubis</i>	Arboreal	21	21	Q 68	—	Hunt (1991b)
<i>Macaca fascicularis</i>	Feed	9	23	Q 74	—	Cant (1988)
<i>Macaca fascicularis</i>	Travel	5	23	Q 65	—	Cant (1988)
<i>Macaca fascicularis</i>	Travel	12	27	Q 60	—	Cannon and Leighton (1994)
<i>Colobus badius</i>	All	3	32	Q 37	—	Gebo and Chapman (1995)
<i>Colobus guereza</i>	All	3	15	Q 41	—	Gebo and Chapman (1995)
<i>Colobus guereza</i>	All	?	37	Q 35	—	Rose (1979)
<i>Colobus guereza</i>	All	?	18	Q 42	—	Morbeck (1977)
<i>Presbytis melalophus</i>	Travel	?	8	L 68	—	Fleagle (1980a)
<i>Presbytis melalophus</i>	Feed	?	30	Q 36	—	Fleagle (1980a)
<i>Presbytis obscura</i>	Travel	?	9	Q 51	—	Fleagle (1980a)
<i>Presbytis obscura</i>	Feed	?	16	Q 69	—	Fleagle (1980a)
<i>Galago senegalensis</i>	All	?	17	L 54	—	Crompton (1983)
<i>Tarsius bancanus</i>	All	?	28	L 66	—	Crompton and Andau (1986)
<i>Tarsius spectrum</i>	All	7	14	L 63	—	MacKinnon and MacKinnon (1980)
<i>Propithecus diadema</i>	All	9	9	L 85	—	Dagosto, pers. com.

¹ACT = activity (travel, feed, arboreal, and all); travel = arboreal movements between trees; feed = movements within a single tree; arboreal = only arboreal movements; all = total movements.²VC = amount of vertical climbing.³CL = amount of overall climbing, includes clambering or generalized climbing and vertical climbing.⁴LOCO = most frequent locomotor type besides climbing (Q = quadrupedalism; BR = brachiation; L = leaping).⁵BR = amount of brachiation.

ception of *Pan paniscus* (Susman, 1984), and certainly not to the extent of the orangutan or some species of gibbons (Table 1). Looked at this way, African apes are not frequent climbers, and if we expect frequent climbing to be an important component of prehomimid behavior, African apes are indeed bad models. This overall perception is clouded, however, by the large terrestrial component to traveling locomotion in African apes. In fact, when African apes move within trees to feed, forage, or to rest, they use climbing frequently, especially vertical climbing (Table 1).

Vertical climbing is a rare behavior among primates (Table 1). In fact, in no primate species except the orangutan and *Ateles geoffroyi* is it a significant component (>10%) of overall locomotor behavior. If only behavior in an arboreal setting is considered, however, gorillas, chimpanzees, *Macaca fascicularis*, and *Papio anubis* also engage in significant amounts of vertical climbing. When arboreal, chimpanzees and gorillas engage in vertical climbing more often than orangutans. In fact, Tuttle and Watts (1985) note that the gorilla, the largest-bodied primate, climbs vertically in 71% of all climbing activities, although large males rarely move into the tree periphery (Remis, 1993). Remis (1995) has also shown gorillas to be very frequent vertical climbers. Even prosimians like tarsiers, indriids, and *G. senegalensis*, habitual users of vertical supports, are moderate vertical climbers relative to the great apes (Table 1). Thus, the behavioral data on great apes to date suggest that they are all good vertical climbers relative to other primates.

Many of the locomotor studies in Table 1 do not distinguish vertical climbing from climbing. Since vertical climbing can only occur on a vertical support, we can also look at frequency of vertical support use to determine the maximum amount of vertical climbing possible. Table 2 shows that only a few primates use vertical supports often, primarily the "vertical clinging and leaping" primates. But in the vertical clinging and leaping forms, frequent vertical support use does not correlate with high frequencies of vertical climbing. For the great apes, almost all climbing sequences are on vertical sup-

ports in the African apes, whereas orangutans use vertical supports during travel 61% of the time (Cant, 1987).

Vertical climbing can only effect movement up or down a vertical support. All living primates are quite capable of performing this action, but they still must be able to move horizontally through the arboreal environment or go to the ground to travel¹ between trees. Chimpanzees, gorillas, and male orangutans travel on the ground (Nissen, 1931; Schaller, 1963; Goodall, 1965; Reynolds, 1965; Lawick-Goodall, 1968; Galdikas, 1979, 1988; Rodman, 1984; Tuttle and Watts, 1985; Hunt, 1992; Doran, 1992, 1993a,b); female orangutans and gibbons travel through the canopy using climbing/clambering, brachiation, or other types of movements. Most arboreal primates travel using quadrupedalism or leaping (Rose, 1973; Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995).

Given this assessment of living primates, a "vertical climbing" protohomimid must have employed another locomotor mode to travel between trees. Stern (1975) suggests that female orangutans, being smaller-bodied, are the best model for travel in this "orangutanian phase" of human evolution. Cant (1987) and Sugardjito and van Hooff (1986) note that female orangutans commonly travel using quadrumanous scrambling, brachiation, and tree swaying, with vertical climbing and quadrupedal walking being rarer movements through the canopy. Forelimb suspension occurred in at least 80% of female orangutan travel bouts (Cant, 1987). Thus, an "orangutanian" or a highly arboreal model for the ancestral protohomimid, based on current locomotor studies, suggests that travel was through the canopy via clambering/climbing and suspensory brachiation, rather than on the ground as in African apes, and that vertical climbing was rare during travel.

To sum up the behavioral record, vertical climbing is an important part of the locomotor repertoire of all great apes in contrast

¹Travel: long-distance movements between trees; normally movements between a series of trees to or from feeding or resting sites (Gebo and Chapman, 1995).

TABLE 2. Vertical support use (VSU) in non-hominoid primates

	VSU, %	References
<i>Galago senegalensis</i>	18	Crompton (1983)
<i>Tarsius bancanus</i>	72	Crompton and Andau (1986)
<i>Tarsius spectrum</i>	65	MacKinnon and MacKinnon (1980)
<i>Propithecus diadema</i>	25	Dagosto, pers. comm.
<i>Saguinus mystax</i>	7	Garber and Preutz (1995)
<i>Saguinus mystax</i>	16	Garber and Preutz (1995)
<i>Saguinus oedipus</i>	26	Garber (1984)
<i>Cebus capucinus</i>	4	Gebo (1992b)
<i>Chiropotes satanas</i>	1	Walker (1993)
<i>Cacajao calvus</i>	4	Walker (1993)
<i>Pithecia pithecia</i>	17	Walker (1993)
<i>Alouatta palliata</i>	2	Gebo (1992b)
<i>Alouatta palliata</i>	10	Mendel (1976)
<i>Cercopithecus ascanius</i>	2	Gebo and Chapman (1995)
<i>Cercopithecus mitis</i>	1	Gebo and Chapman (1995)
<i>Cercopithecus aethiops</i>	2	Rose (1979)
<i>Cercocebus albigena</i>	5	Gebo and Chapman (1995)
<i>Colobus badius</i>	4	Gebo and Chapman (1995)
<i>Colobus guereza</i>	3	Gebo and Chapman (1995)
<i>Colobus guereza</i>	2	Rose (1979)
<i>Colobus guereza</i>	2	Morbeck (1977)

to other primates, including gibbons. This observation implies that the anatomical adaptations associated with vertical climbing most likely postdate the divergence of hylobatids, since gibbons are not frequent vertical climbers. Further, African apes use vertical climbing less frequently than orangutans, but only because so much of their locomotor behavior takes place on the ground. When only arboreal locomotion is considered, African apes use vertical climbing more frequently than orangutans, and thus cannot be viewed as poorer examples of a protohominid than an orangutan in terms of climbing behavior. Thus, African apes can in fact represent a good model for the pre-bipedal stage, even if vertical climbing is linked to bipedalism (Prost, 1980; Fleagle et al., 1981). It is not climbing, but traveling locomotion, that best divides the living apes into discrete groups. Gibbons travel using brachiation. Orangutans travel via scrambling, brachiation, and tree swaying. Among orangutans, only males use the ground for traveling over long distances, and that only occasionally (Galdikas, 1979, 1988; Rodman, 1984). For the African apes, travel is by terrestrial quadrupedalism (i.e., knuckle-walking).

Kinematics

Is vertical climbing in apes a fundamentally different type of climbing? In the

search to explain the pre-bipedal stage, kinematics has been used to distinguish various patterns of hindlimb function among non-human primates. These kinematic studies have failed to show any great similarity between primate and human bipedalism (Elftman, 1944; Jenkins, 1972; Ishida et al., 1975, 1984; Vangor, 1979; Kimura et al., 1979; Prost, 1980), but have surprisingly demonstrated a connection between human bipedalism and vertical climbing (e.g., Prost, 1980; Vangor and Wells, 1983; Yamazaki and Ishida, 1984), leading to the idea that vertical climbing is preadaptive for and a critical functional behavior prior to the evolution of human bipedalism (Fleagle et al., 1981).

Fleagle et al. (1981) note that chimpanzees are adept climbers, and Prost (1980) states "The segment relations of the lower limbs of a chimpanzee vertically climbing mimic those of humans walking" (Prost, 1980, p. 181). So, why have African apes been neglected as potential protohominid models? One reason may be that human hip musculature is not as similar to chimpanzees as it is to other primates, especially *Alouatta* and *Pongo* (Stern, 1971, 1975). Another reason may be that African apes are more often terrestrial quadrupeds than climbers. Last, Stern (1971, p. 305) and Fleagle et al. (1981, p. 372) reject the use of any extant ape as a model. All three explanations seem to be poor reasons to exclude chimpanzees as a

potential model, since chimpanzees are specifically used by Prost (1980) to show that vertical climbing, even with a "different type" of hip musculature, is very similar to human bipedalism. Likewise, although African apes are frequent users of terrestrial quadrupedalism, both chimpanzees and gorillas are frequent or adept climbers when in trees, as noted above. Finally, African apes, especially chimpanzees, are phylogenetically the closest living relatives of hominids (Ruvolo et al., 1991). Thus, the kinematic evidence provides no grounds for neglecting the highly terrestrial African apes as potentially good models for the prebipedal stage of human evolution.

I would take kinematic studies one step further and ask, Do apes differ fundamentally from other primates in limb function during vertical climbing sequences? If apes, especially Asian apes, are truly better or more efficient climbers than other primates, the advocates of the vertical-climbing hypothesis could use this assessment to exclude the highly terrestrial African apes or other primates as potential models. Unfortunately, wide-ranging kinematic testing on apes has yet to be performed. Hirasaki et al. (1993) compared vertical climbing sequences in *Ateles* with those of *Macaca* and noted that during vertical climbing *Ateles* utilized a more erect trunk, more extended lower limb joints, more forceful hindlimbs, larger horizontal forces, longer strides, and a synchronized forelimb (ipsilateral movement sequences) compared to *Macaca*. Most differences are of degree rather than being qualitative, with the exception of the ipsilateral limb use. In fact, one might have expected greater overall differences given the substantial anatomical differences in body shape, limb lengths, and joint mobility between these two taxa. Hunt (1992, p. 91) also noted that "the kinematics of baboon and chimpanzee vertical climbing differed little." Thus, the question remains, are hindlimb vertical climbing sequences in chimpanzees (Prost, 1980) or gibbons (Yamazaki and Ishida, 1984) fundamentally different from those of monkeys?

The stick-figure diagrams of climbing sequences in Prost (1980, Fig. 5), Hirasaki et al. (1993, Fig. 3), and Yamazaki and Ishida

(1984, Fig. 1) suggest that *Hylobates*, *Ateles*, and *Macaca* utilize more flexed knees throughout a vertical climbing sequence whereas *Pan*, *Hylobates*, and *Ateles* use more erect trunks. The hindlimb sequences of *Hylobates* and *Ateles* appear to be the most similar. These admittedly cursory observations imply some kinematic differences between apes and ape/monkey vertical climbing. If the advocates of the vertical-climbing model are correct, they need to specify how the kinematic climbing pattern in apes and perhaps African apes is qualitatively different from other living primates (e.g., in manifesting less flexed knees in chimpanzees) and why these differences necessarily exclude specific apes as potential models for the prebipedal phase of hominid bipedalism. Although kinematics might help to resolve certain problems associated with the evolution of bipedalism, this approach has so far neither explained how subtle differences in climbing movements can be divided into meaningful mechanical or functional differences across primates nor accounted for any of the morphological differences between primates.

THE MORPHOLOGICAL RECORD

When does frequent climbing appear in the paleontological record of catarrhines?

Adaptations for increased climbing ability date to the earliest Oligocene (Fleagle, 1980b, 1983; Fleagle and Simons, 1978, 1982a,b; Gebo, 1989; Gebo et al., 1994). For example, the robust and long first metatarsals and deep calcaneocuboid pivot joints characteristic of living and extinct hominoids are all present in propliopithecids (Gebo and Simons, 1987; Gebo, 1989). These early catarrhines have long been envisioned as *Alouatta*-like in their locomotor profile, being frequently described as cautious quadrupedal-climbers (Preuschoft, 1974; Fleagle et al., 1975; Conroy, 1976a,b; Schön Ybarra and Conroy, 1978; Ford, 1988; Rose, 1988a, 1989; Fleagle and Simons, 1978, 1982a,b; Fleagle, 1983; Gebo and Simons, 1987; Gebo, 1989, 1993). The same categorical description applies equally well to early Miocene hominoids like *Proconsul* (e.g., Mor-

beck, 1975, 1976; Feldesman, 1982; Harrison, 1982; McHenry and Corruccini, 1983; Rose, 1983, 1986, 1993; Fleagle, 1983; Walker and Pickford, 1983; Langdon, 1984, 1985; Begun, 1987; Walker and Teaford, 1989; Gebo, 1989; Rose et al., 1992; Ward, 1993; Ward et al., 1993; Begun et al., 1994). Most living catarrhine monkeys have lost or reduced a series of anatomical features related to increased muscularity or joint mobility associated with increased climbing abilities (Fleagle and Simons, 1982a; Rose, 1988a; Strasser, 1988; Harrison, 1989). Thus, versatile climbing and the osteological adaptations that have been attributed to this locomotor pattern predate the frequent climbing behavior of great apes by 25 million years or more, and accordingly cannot explain the unique features of the ape forelimb and thorax.

Are the unique body characteristics of living apes best explained as adaptations for vertical climbing?

Living apes, as well as the extinct *Oreopithecus* (Straus, 1963; Tuttle, 1975; Harrison, 1986; Sarmiento, 1987), share features of thorax and forelimb shape which distinguish them from other non-atelin (Fig. 2) primates. These features (Table 3; Figs. 3–6) have been well documented for apes (Keith, 1903, 1923; Straus, 1930; Napier and Davis, 1959; Schultz, 1960, 1968; Cartmill and Milton, 1977; Lewis, 1969, 1974; Tuttle, 1969a,b, 1975; Rose, 1983; Harrison, 1986; Sarmiento, 1987) and have additionally been analyzed as adaptations to vertical climbing (Fleagle et al., 1981). It is curious, however, that gibbons, which share all of the key forelimb and thorax anatomy with great apes (Table 3; although some features vary by degree of expression, Table 4), are not particularly frequent vertical climbers (Table 1). Instead, they are the most frequent users of suspension and brachiation. Although great apes and humans brachiate² much less than do gibbons, all can perform this behavior compared to non-atelin primates, which cannot. Further, Stern (Table 1, 1975) noted that the special similarities of human hip and thigh musculature is in fact more similar to that of *Alouatta*, a non-frequent vertical climber (Table 1), than to *Ateles* or to *Pongo*.

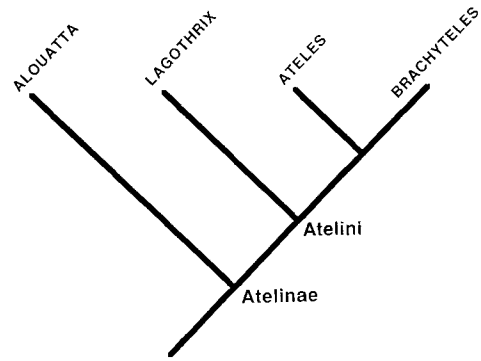


Fig. 2. Evolutionary relationships of the atelines.

This observation implies that the special role attributed to vertical-climbing adaptations in linking human and orangutan hip and thigh musculature is called into question.

Like apes, atelines (*Alouatta*, *Lagothrix*, *Ateles*, and *Brachyteles*) rely on climbing and suspension in their arboreal positional behavior (Table 1; reviewed in Stern, 1971; Mittermeier, 1978; Fleagle, 1980a; Cant, 1986, 1987; Schön Ybarra and Schön, 1987; Hunt, 1991b; reviewed in Tuttle, 1986). Like the orangutans, atelines also suspend quite often by their hindlimbs, with or without the use of their prehensile tails (Stern, 1971; Mittermeier, 1978; Schön Ybarra, 1984; Cant, 1986; Schön Ybarra and Schön, 1987; Rosenberger, 1983; Gebo, 1992b; Strier, 1992). Furthermore, the Atelini, that is *Lagothrix*, *Ateles*, and *Brachyteles*, are quite capable of brachiating and using manual suspension (Erikson, 1963; Stern, 1971; Stern and Oxnard, 1973; Mittermeier, 1978; Jenkins et al., 1978; Stern et al., 1980a,b; Jungers and Stern, 1981; Grand, 1984; Cant, 1986; Strier, 1992).

²Brachiation, as defined here, represents slow to moderate pendular arm-swinging where the trunk undergoes rotation under the supporting hand (Avis, 1962; Fleagle, 1974; Jungers and Stern, 1983; Larson and Stern, 1986). This differs from fast or ricochet brachiation as defined by Tuttle (1969b) by speed of action and by the absence of an aerial phase. Other forms of arm-swinging or bimanualism used by indriids, colobines, and other primates where generally elbows are bent, trunks are non-rotating, and the sequence of movement is very brief are best viewed as alternative representations of simple arm-swinging.



Fig. 3. Ape thorax (*Hylobates*). Note the broadened thorax and the dorsal position of the scapulae for living apes.

Climbing and hindlimb suspension are commonly observed behaviors within atelines. These two positional behaviors are also found in a variety of other primates, especially pitheciines (Stern, 1971; Walker, 1993) and prosimians (Jolly, 1966; Tattersall, 1982; Crompton, 1984; Gebo, 1987; Dagosto, 1994). However, the Atelini differ from their close relative, *Alouatta*, and other climbing and hindlimb-suspensory primates, in their ability to brachiate or suspend uni- or bimanually, abilities that distinguish the living apes and humans from other catarrhines.

Many "hominoid-like" features of upper body anatomy distinguish the Atelini from the more primitive ateline *Alouatta* (Table 3). Erikson (1963), in particular, documented this similarity in ape and ateline body forms, as have many other authors (e.g., Schultz, 1930, 1956; Napier and Davis, 1959; Hill, 1962; Ashton and Oxnard, 1963; Schön,

1968; Oxnard, 1963, 1967; Stern, 1971, 1975; Ankel, 1972; Roberts, 1974; Stern et al., 1977, 1980a,b; Jenkins et al., 1978; Schön and Ziemer, 1978; Ziemer, 1978; Jenkins 1981; Sarmiento, 1983; Ford, 1986; Schön Ybarra and Schön, 1987; Grand, 1968a,b; Jungers and Stern, 1981; Gebo, 1989; Rosenberger and Strier, 1989). However, *Alouatta* is morphologically very distinct from the Atelini (Table 3). They possess different thorax (Fig. 7) and upper limb anatomies (Figs. 8–11), which distinguish the brachiating atelins from the non-brachiating *Alouatta*. Clearly, a relationship must exist between the unusual upper body and forelimb anatomy of living apes and Atelini with brachiation and forelimb suspension, a rather peculiar positional behavior for primates. In the following sections, I will argue that brachiation and arm suspension, as originally suggested by Keith (1903, 1923), Gregory (1916, 1927a,b, 1928a,b), and Morton (1924b), provide a better explanation for the evolution of the ape body plan than does vertical or generalized climbing. A review of the most distinctive traits follows below.

Thorax. Schultz (1936, 1973) documented that relative to trunk length, chest circumference is much wider and deeper in living apes and humans than in other primates. The broad thorax even extends dorsally beyond the bodies of the thoracic vertebrae with the first seven ribs being sharply bent ventrally (Schultz, 1960, 1973). The manubrium is also much wider in living apes and humans (Schultz, 1936, 1968, 1973). This combination of a wide transverse chest diameter and great rib curvature shapes the ape and human thorax into a barrel-shaped form in gibbons (Fig. 3) and humans and a more funnel-shaped form in great apes (Schultz, 1961). Further, the wide ilia of the living apes and humans contribute to the general widening of the trunk (Schultz, 1930, 1936, 1973). The reduced number of lumbar vertebrae, tail loss, and visceral peculiarities (e.g., mesocolic and pericardial mesenteries) of the living apes and humans have been associated with reduced flexibility in the back and a more erect body posture (orthogrady) (Keith, 1903, 1923; Schultz, 1969, 1973; Cartmill and Milton, 1977; Sha-

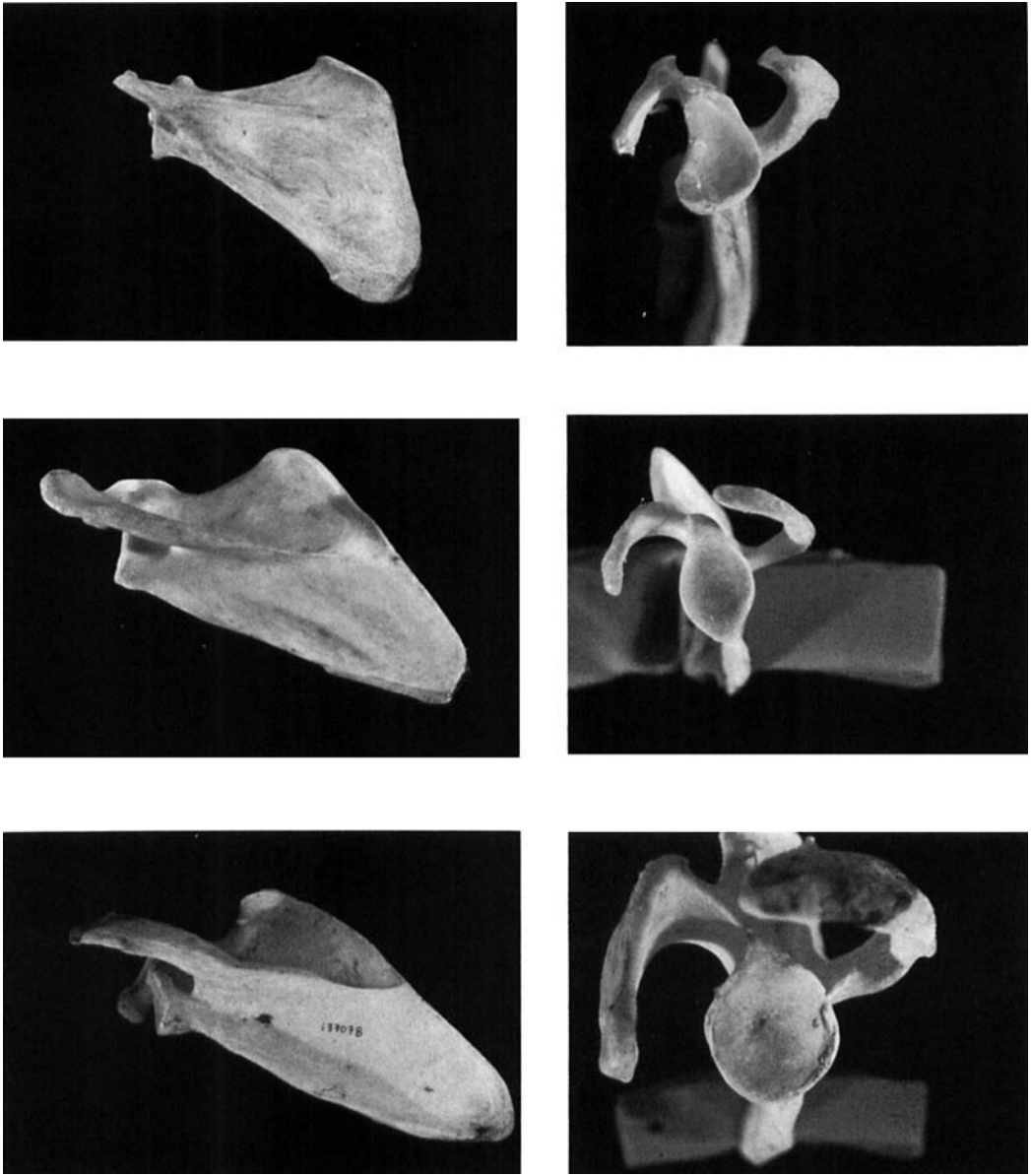


Fig. 4. Ape scapulae. A dorsal view of scapulae and a lateral view of the glenoid fossa for a colobine (**top**), *Hylobates* (**middle**), and *Pan* (**bottom**). Note the narrow triangular shape change of the ape scapulae along with the round glenoid fossa compared to these same features in the colobine.

piro, 1993). A widened thorax and manubrium also characterize the Atelini (Table 3).

Some (e.g., Stern, 1975; Fleagle, 1976; Fleagle et al., 1981) have linked the unusual torso and forelimb anatomy of atelines and apes to vertical climbing, especially as it may relate to the use of large-diameter supports

(Cartmill, 1974; Jungers, 1977, 1978). However, the most recent studies on chimpanzees do not support this behavioral link. In fact, Kano (1992), Hunt (1992, 1994), and Doran (1993b) have all shown that vertical climbing occurs most often on small-diameter supports in chimpanzees. Cant (1987) likewise



Fig. 5. Ape proximal humeri. Anterior and posterior views of proximal humeri for a colobine (**left**), *Hylobates* (**middle**), and *Pan* (**right**). Note the enlarged globular humeral head and reduced tubercles in the apes along with the torsional shift of the line of orientation of the humeral head relative to the shaft in the ape humeri.

notes that climbing on large tree supports occurred only 2.3% of the time in orangutans. In *Ateles*, vertical climbing occurs most often on branches and medium-sized substrates (Mittermeier, 1978; Cant, 1986), not the larger-diameter supports. Thus, vertical climbing on larger-diameter supports does not appear to be a satisfactory explanation for these features (see also Hunt, 1992).

Forelimb. Because the thorax of living apes and humans is broad, the scapula has been repositioned dorsally (Fig. 3) changing the orientation of the glenoid fossa to the more lateral and cranial position (Schultz, 1936; Roberts, 1974), and keeping the shoulders well away from the midline of the body. The glenoid fossa is also more rounded in overall shape (Fig. 4). Cartmill and Milton



Fig. 6. Ape distal humeri. Anterior views of the distal humerus in a colobine (left), *Hylobates* (middle), and *Pan* (right). Note the spoon-shaped trochlea in the apes.

(1977, p. 266) "suggest that a transversely broad thorax may reflect not body size per se, nor yet upright posture, as Keith ('23) originally claimed, but a need for increased shoulder mobility; having a broad thoracic cage redirects the glenoid sockets laterally and moves them further apart, and so increases the span of the arms and their range of circumduction." This suggestion fits well with ape and *Ateles/Brachyteles* proximal humeral anatomy since all possess expanded joint surfaces to increase shoulder mobility (Fig. 8).

Living hominoids also display distinctive scapular shapes compared to other primates (Fig. 4) in that they possess a long vertebral border and a shorter transverse dimension (Schultz, 1968; Roberts, 1974). The scapulae of gibbons and chimpanzees are more narrowly triangular in appearance than are those of orangutans, gorillas, and humans. Furthermore, the acromion process is long and wide and the clavicle is elongated in living apes and humans in response to the broad thorax and the dorsal scapular position relative to other primates (Gregory, 1928a; Schultz, 1968, 1969, 1973). Hominoid clavicles vary in curvature with orangutans having fairly straight bones (Schultz, 1930). All are widened toward the acromion.

In the Atelini, scapulae are also dorsally located, narrowly shaped, and possess a round glenoid fossa in contrast to *Alouatta* (Figs. 7, 9). The Atelini also possess widened clavicles. However, *Lagothrix* is intermedi-

ate in its body plan between that of *Ateles/Brachyteles* and *Alouatta*. *Lagothrix* shares with *Ateles* and *Brachyteles* a somewhat widened thorax, manubrium, and clavicle, and a more dorsal scapular position, but lacks long humeri, large globular humeral heads, and the long hands of *Ateles* and *Brachyteles* (Erikson, 1963). Scapular shape and humeral torsion in *Lagothrix* are also intermediate in their resemblances to *Ateles* and *Alouatta*. Rosenberger and Strier (1989) list a variety of other features held in common by *Ateles* and *Brachyteles* (e.g., a vestigial thumb, long curved metacarpals, a highly oblique scapular spine, and a reduced acromion).

Living apes are known for the great length of their forelimbs. Schultz (1956) has shown that Asian apes have much higher intermembral indices than African apes or humans (Schultz, 1956; Tuttle, 1975; Aiello and Dean, 1990). Brachial indices are highest among the frequent arm-swinging primates (Schultz, 1937; Erikson, 1963). *Ateles* and *Brachyteles* also possess elongated humeri and ulnae (Erikson, 1963).

At the proximal humerus, living apes and humans possess a large globular humeral head, which is twisted relative to the shaft (medial torsion), with low closely positioned small tubercles (Fig. 5; Gregory, 1928a; Miller, 1932; Rose, 1989). The low and smaller tubercles allow a greater degree of upward mobility for the humerus (Larson and Stern, 1989). Medial torsion is least ex-

TABLE 3. Upper body and forelimb specializations of living apes compared to atelines and lorises¹

Apes	<i>Ateles/</i> <i>Brachyteles</i>	<i>Lagothrix</i>	<i>Alouatta</i>	Lorises
Thorax				
Broad thorax	*	*	—	—
Ribs—high degree of angulation	*	*	—	—
Widened manubrium	*	*	—	—
Long clavicle	—	—	—	—
Dorsally positioned scapula	*	*	—	—
Long vertebral scapular border	*	*	*	*
Upper limb				
Long length	*	—	—	—
Long and straight humeral shaft	*	—	—	—
Long forearm	*	—	—	—
Shoulder				
Cranially oriented glenoid fossa	*	*	—	—
Long and wide acromium	—	—	—	—
Large globular humeral head	*	—	—	*
Reduced humeral tubercles	*	—	—	*
Moderate medial torsion	*	*	—	—
Narrow bicipital groove	*	—	—	—
Elbow				
Deep olecranon fossa	—	—	—	—
Spool-shaped trochlea	—	—	—	—
Round capitulum	—	—	—	*
Reduced olecranon process	*	—	—	—
Broad semilunar notch	*	—	—	—
Circular radial head	*	—	—	*
Wrist				
Short styloid process	—	—	—	—
Broad ulnar head	—	—	—	*
Meniscus	—	—	—	—
No pisiform-ulnar articulation	—	—	—	*
Lower body				
Short lumbar region	*	*	*	—
Widened ilia	*	*	*	—
Reduced tail	—	—	—	*
Visceral adhesions				
Mesocolic	*	—	—	—
Pericardial	*	—	—	—

¹ Features shared by *Ateles* and *Brachyteles* with the living apes to the exclusion of *Alouatta* and lorises are likely related to brachiation, arm suspension, and orthograde. *Lagothrix* is intermediate between *Alouatta* and *Ateles/Brachyteles* in its possession of ape-like features. * = features present; — = features absent.

pressed in gibbons and most expressed in humans (Larson, 1988). Likewise, *Ateles* and *Brachyteles* possess globular humeral heads with slight medial torsion (Fig. 8). Thus, both the living apes and humans and *Ateles* and *Brachyteles* have expanded the proximal humerus for greater shoulder mobility and have had to twist the humeral head to maintain contact with the more dorsally positioned scapulae.

Distally, a spool-shaped humeral trochlea (Fig. 6) provides stability for hyperextension of the hominoid forearm (Jenkins, 1973; Rose, 1988a, 1993), while the radiohumeral joint facilitates extreme forearm rotation (Rose, 1988a, 1993; Sarmiento, 1988). Features related to hyperextension of the forearm include a deep humeral coronoid fossa,

well-developed medial and lateral trochlear keels, a reduced olecranon process, and extensive caputular development posteriorly (Rose, 1993).

Likewise, the Atelini possess a reduced olecranon process (Fig. 8), although not to the degree of the living apes. All atelines lack a spool-shaped trochlea at the distal humerus (compare Figs. 6 and 11). Thus, extension of the forearm is not as well developed in atelines as in apes, nor is the elbow as functionally stable in these monkeys. However, elbow stability may not be as functionally critical for the Atelini during arm suspension, since all possess a prehensile tail which probably reduces forelimb stress and thus reduces the need for greater elbow stability while hanging.

TABLE 4. *Distinctive upper body features of living apes and humans*¹

	Hylobates	Pongo	Gorilla	Pan	Homo
Thorax shape	Barrel-shaped	Funnel-shaped	Funnel-shaped	Funnel-shaped	Barrel-shaped
Scapular shape	Narrow triangular	Broad triangular, small supraspinous fossa	Broad triangular	Narrow triangular	Broad triangular
Clavicular curvature	Convex	Straight	Concave	S-shaped	S-shaped
Intermembral index	126–147	139	115–116	103–107	88
Brachial index	110–115	101	80–81	92–94	76
Humeral torsion (degrees)	128–145	120–162	154–173	139–159	141–178
Lateral trochlear keel development	Moderate	Well-developed	Well-developed	Well-developed	Moderate
Meniscus	Semilunar meniscus and nonarticular triangular ligament	Fused meniscus–ulnocarpal ligament	Triangular disc	Semilunar meniscus and triangular articular ligament	Triangular disc
Ulnotriquetal contact	Partly	None	None	Partly	None
Hands	Long, grasping	Suspensory	Knuckle-walking	Knuckle-walking	Manipulative, expanded apical tufts

¹ REFERENCES: Aiello and Dean (1990); Cartmill and Milton (1977); Jungers (1984); Larson (1988); Lewis (1972a–c); Rose (1988a); Sarmiento (1988); Schultz (1930, 1961); Tuttle (1967, 1969b).

From his work on chimpanzee positional behavior, Hunt (1991a) has argued that the mechanical design of the ape thorax and forelimb are adaptive complexes related to arm suspension and vertical climbing. He believes that the osteoligamentous adaptations in the upper bodies and forelimbs of apes are adaptations for arm suspension (see also Keith, 1923), but follows Fleagle et al. (1981) in explaining the novel muscular adaptations occurring in living apes as responses to vertical climbing. According to Hunt (1991a,b), these two positional behaviors, arm suspension and vertical climbing, are the only two behaviors that unite all living hominoids. This suspension/vertical climbing model does not, however, explain the shoulder movement of circumduction, which all living apes and humans can perform. Circumduction is not a movement which is necessary for vertical climbing since all primates, even those that cannot circumduct, can vertically climb. Nor is this particular movement necessary for arm suspension. Again, non-brachiating primates can both climb vertically and arm-suspend without any special anatomical features that differ from the general climbing adaptations

of primates (cf. Jenkins et al., 1978). Only primates that are capable of brachiating have the ability to circumduct at the shoulder joint.

Another problem with Hunt's (1991a) argument concerns the remodeling of the upper body of apes in response to a postural adaptation. Although some postural adaptations are apparent in primates (e.g., ischial callosities or prehensile tails), none have required such a wholesale remodeling of body shape as is the case in the ape body plan. Postures just do not appear to be critical behaviors in terms of stress, limb structure, and adaptation (Prost, 1965, 1980; Oxnard, 1974; Reynolds, 1985; Nordin and Frankel, 1989; Gunther et al., 1991). Prolonged arm suspension may be a different matter, but arm suspension by itself does not appear sufficient to explain the extensive amount of morphological change observed in the upper body and forelimbs of living apes. Thus, neither the ability to climb vertically nor the possession of adaptations necessary for vertical climbing distinguish the living apes from their ancestors, which possessed a different, more monkey-like type of body form (Rose, 1983; Ward, 1993). It is the special

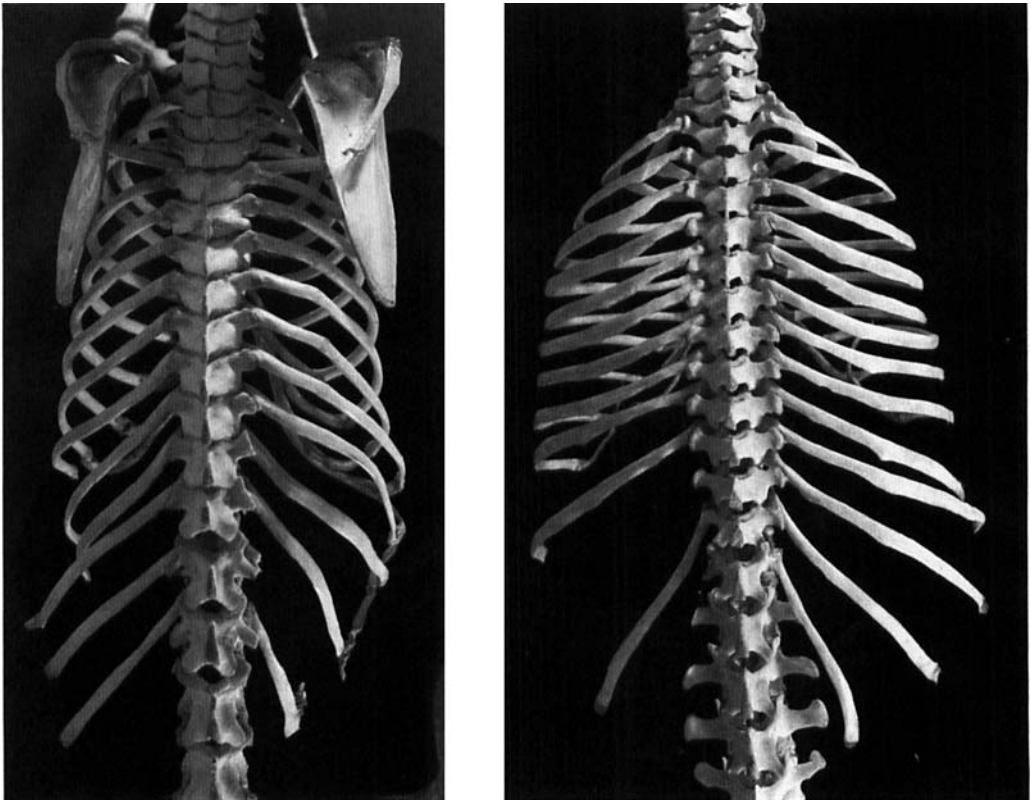


Fig. 7. Ateline thoraxes. Dorsal view of the thorax of *Alouatta* (left) and *Ateles* (right). Note the long, narrow, and dorso-ventrally deep thorax of *Alouatta* compared to the mediolaterally widened and dorsoventrally shallow thorax of *Ateles*.

adaptations for prolonged arm suspension and brachiation that distinguish the living apes from their ancestral condition.

Besides the many osteological features noted above, there are a variety of muscular and ligamentous adaptations in the forelimb that distinguish living apes and humans from other primates (e.g., the distal insertion of the deltoid; see Keith, 1923; Gregory, 1928b; Straus, 1930; Miller, 1932; Ashton and Oxnard, 1963, 1964; Tuttle, 1969b, 1970). Electromyographic studies by Stern and his colleagues have also documented aspects of muscle form and activity in the arm-hanging and brachiating Atelini that differ from that of *Alouatta* (Stern et al., 1977; Stern et al., 1980a,b). For example, Stern and his colleagues examined the caudal digitations of serratus anterior and its electromyographic activity in *Alouatta*, *Lagothrix*,

and *Ateles*, and noted that more craniocaudal orientations of this muscle occurred in brachiating and arm-hanging primates (e.g., *Lagothrix* and *Ateles*), including the living apes (Stern et al., 1980a).

When examining shoulder function in brachiating primates, Jenkins et al. (1978, p. 75) stated that "Brachiating and quadrupedal climbing entail fundamentally different kinds of shoulder excursion." They further document that "Climbing up and down and moving along a complex, linear arrangement of arboreal substrates also require a substantial range of forelimb adduction and abduction, but for this the generalized mammalian shoulder is preadapted" (p. 75). Thus, the upper body and forelimb anatomy of *Alouatta* is well adapted for climbing activities, even vertical climbing, but this same region has been modified in the Atelini. The



Fig. 8. Ateline humeri and ulnae. **Top:** Posterior views of *Alouatta* (left) and *Ateles* (right) humeri. Note the long length of the humerus as well as the enlarged humeral head for *Ateles* in comparison to *Alouatta*. **Below:** Medial and anterior views of ulnae. Note the long length of the ulna and the reduced olecranon process in *Ateles* (right) compared to *Alouatta* (left).

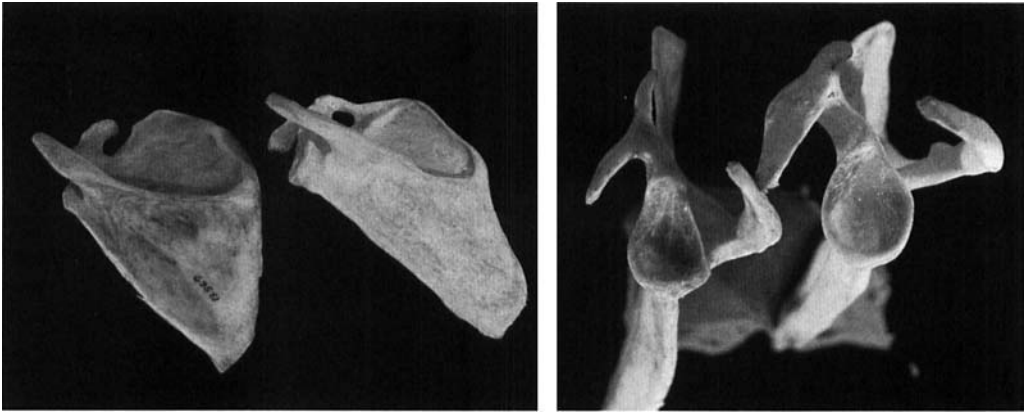


Fig. 9. Ateline scapulae. Dorsal and lateral views of *Alouatta* (left) and *Ateles* (right) scapulae. Note the narrower triangular shape of the scapula as well as the round glenoid fossa in *Ateles* compared to *Alouatta*.



Fig. 10. Ateline clavicles. Cranial view of *Alouatta* (top) and *Ateles* (below) clavicles. Note that both are similar in length but that *Ateles* possesses a much wider clavicle, especially at the acromial end.

only reasonable explanation for these upper body modifications in the Atelini, relative to *Alouatta*, is that they are the result of arm suspension and brachiating capabilities.

In the wrist, the shortened ulnar styloid process and the intra-articular meniscus greatly facilitate adduction of the hand in living apes and humans (Lewis, 1969, 1971,

1972a–c, 1974). Further, the hominoid wrist facilitates a unique degree of forearm rotation of 150° compared to other primates due to a modified proximal carpal row and distal radioulnar joint (Sarmiento, 1988). In all, the hominoid wrist is a unique functional complex possessed solely by living hominoids (Lewis, 1969, 1972a–c, 1974; Cartmill and Milton, 1977; Sarmiento, 1988).

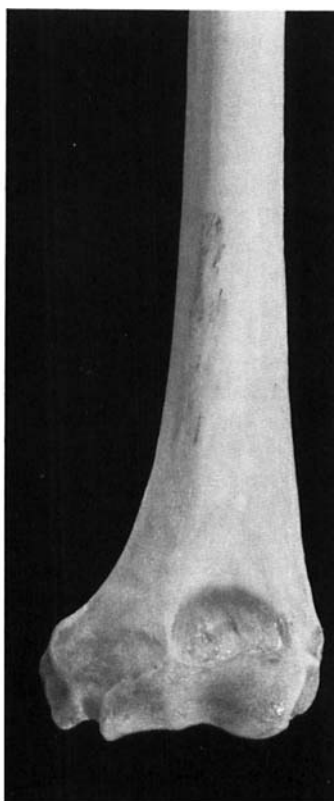
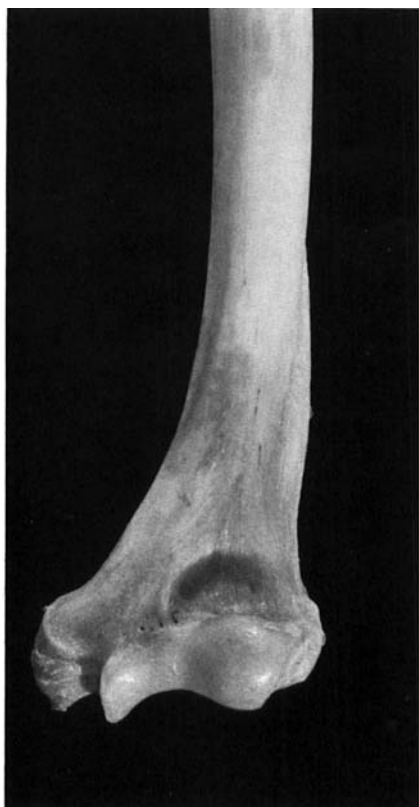
Cartmill and Milton (1977) implied that great ape wrist morphology was more likely to be related to climbing than to brachiation. Cartmill and Milton (1977, p. 265) suggest that “reduction or loss of the ulnocarpal articulations, in the larger apes as well as in lorises . . . , is related to the fact that these animals do not ordinarily leap across gaps between branches, but bridge them by stretching across and grabbing the support ahead before relinquishing the one behind.” Thus, the versatile and suspensory climbing abilities of lorises, including bridging between supports, are similar to how orangutans move. More recent field studies on the great apes, however, show that only orangutans bridge or transfer across gaps to other arboreal supports often, whereas African apes simply knuckle-walk along the ground to move between trees (Tuttle, 1986). Thus, bridging or transferring between supports does not seem to be a behavior which can be universally associated with the loris/ape form of wrist anatomy. Lewis (1972a–c, 1974), in particular, has argued that these wrist features are associated with brachiation in apes. Lorises further lack all of the key upper body and forelimb modifications of the living apes and Atelini. The long vertebral scapular border and globular humeral heads of lorises are features shared with atelines and apes, and thus only may be related to increased forelimb mobility, an ability associated with many behaviors. Wrist features shared by lorises and apes are also likely to be associated with increased mobility, a very general function that is necessary for the performance of a number of biological roles, (e.g., climbing, bridging, and brachiation).

Jenkins (1981) also documented that brachiation and forelimb suspension in primates are facilitated by a rotatory midcarpal joint. This joint structure is found in *Ateles*,

Lagothrix, *Hylobates*, and *Pongo*, but not in *Alouatta*. Jenkins (1981) reports that the African ape midcarpal joints would not be categorized as being similar to *Hylobates*, although wrist radiographs of sedated chimpanzees reveal mid-carpal pronation and supination abilities. Thus, primates can climb with or without mid-carpal rotation, but only primates with mid-carpal rotation can brachiate.

Comparing ape and human upper limb and thorax morphology with that of the Atelini, especially *Ateles* and *Brachyteles*, suggests that brachiation and arm suspension is a better explanation for the novel upper-limb and thorax features of living apes than vertical climbing. The Atelini also differ from living apes in a variety of upper-body features, indicating that this is a clear case of functional convergence. Ziemer (1978) has shown that *Ateles* and *Lagothrix* possess low values for forearm extension (108°) and that complete extension at the elbow is impossible, which is likely to be due to the length of the olecranon process (Fig. 8). Radial rotation was measured at 129° in *Lagothrix* (Ziemer, 1978) versus 150 – 163° in hominoids (Sarmiento, 1988). The long styloid process of the ulna in the Atelini (Fig. 11) also limits ulnar deviation compared to the apes (about 40° vs. 70 – 98° ; Ziemer, 1978). Scapular shape, clavicular width and curvature, lower thorax shape, vertebral shape, shoulder, elbow, and wrist morphology all exhibit a variety of anatomical differences relative to living apes (compare Figs. 3–6 with 7–11). Thus, thorax and forelimb morphology evolved independently in these two lineages, and ateline evolution illustrates the transition from a quadrupedal-climbing ancestral condition (*Alouatta*) to a forelimb-suspensory and brachiating common ancestor of Atelini.

In this way, a comparison of Atelini with *Alouatta* mirrors a comparison of the body plan of living apes with that of early Miocene hominoids like *Proconsul*. The ability to brachiate and to arm-suspend over prolonged time periods does require an unusual upper body form. Only the Atelini and living apes utilize these two behaviors. Although both *Ateles* and the great apes also vertically climb, so do many other primates, none of



which exhibit these features. If nothing else, pushing the shoulders out away from the midline of the body, as well as twisting the humeral head, are rather peculiar ways to enhance climbing abilities, since no other frequently climbing primates or frequently vertically climbing primates (e.g., *Macaca fascicularis* or *Papio anubis*) have adopted this type of anatomical design. Thus, it seems simpler to harken back to the message of Keith (1923) in which he suggested that the mechanical design of the ape and human thorax, as well as the unique forelimb adaptations, are primarily due to increased mobility at the shoulder and relate to brachiation and prolonged arm suspensory capabilities.

What are the advantages of arm suspension for living primates?

Most primates extend their foraging radius by hanging below supports with their hands, feet, or combinations of both. Foot or hindlimb suspension is the more common method of suspension in primates. Many prosimians, including lorises, cheirogaleids, or lemurs (especially *Varecia*), as well as pitheciines and atelines are notable examples (Jolly, 1966; Stern, 1971; Stern and Oxnard, 1973; Mittermeier, 1978; Tattersall, 1982; Crompton, 1984; Schön Ybarra, 1984; Gebo, 1987; Strier, 1992; Walker, 1993; Dagosto, 1994). Even the subfossil indriid *Paleopropithecus* appears to have adopted a more sloth-like approach involving quadrupedal suspension rather than adopting uni- or bi-manual suspensory abilities (Carleton,

1936; Walker, 1974; Jungers, 1980; Gebo, 1986; Godfrey, 1988). Only the atelines and *Cebus* have evolved prehensile tails (Rosenberger, 1983) for below-branch foraging. Thus, most primates have taken a different evolutionary path in body suspension than those of the living apes and Atelini, which emphasize forelimb suspension.

Examining the body plan of an early Miocene hominoid like *Proconsul*, which lacks any specialized forelimb lengthening, suggests that these early Miocene hominoids were better suited for quadrupedal suspension or even hindlimb suspension, given their limb anatomy and body configuration (Morbeck, 1976; Rose, 1983, 1993; Sarmiento, 1983; Walker and Pickford, 1983; Ward, 1993; Ward et al., 1993), if the foraging radius needed to be expanded. Why was there a shift in hominoid evolution toward the rather unusual solution of forelimb lengthening?

Grand (1972, 1984), Temerin and Cant (1983), Cant (1986), and more recently Hunt (1991a,b) have argued that there are many advantages in lengthening the forelimb for arm suspension, although others have viewed forelimb lengthening in apes as being derived from size increases rather than being due to a specific behavior (see Biegert and Maurer, 1972; Delson and Andrews, 1975; Jungers, 1985). Long arms, as Napier (1967) argued, are also beneficial with increasing body size. As body size increases relative to the diameter of the support, this tends to force a primate to hand below supports, rather than allowing it to balance on top of a support (Napier, 1967; Cartmill, 1974, 1985). Arm suspension/brachiation is typically used on small-diameter supports (Napier, 1967; Cant, 1987; Hunt, 1992; Doran, 1993a). Grand (1972) further discussed the increased foraging radius that gibbons possess with their extensively elongated arms, as well as the reduced energy expenditure, which minimizes body readjustments while foraging as observed in non-arm-hanging primates like macaques. Grand (1984) also argued that *Hylobates* and *Ateles* possess greater choices of travel routes owing to their forelimb suspensory abilities than do quadrupedal primates. Similar suggestions were made by Cannon

Fig. 11. Ateline distal humeri and ulnae. Anterior view of distal humeri and a lateral view of distal ulnae for *Alouatta* (left) and *Ateles* (right). Note that the distal humerus and ulna of atelines is quite unlike the morphological appearance of these same structures in the living apes. For example, no ateline possesses a spool-shaped trochlea, and the styloid process is not reduced. Neither is the distal ulnar head enlarged as in living apes. In fact, the styloid process is well-buttressed and the distal articular facet greatly expanded in *Ateles* compared to *Alouatta*, a very different morphological appearance compared to living apes. Further, the greater medial curvature of the humeral shaft and the downturned lateral rim of the humeral trochlea in *Alouatta* contrasts greatly in comparison to these same structures in *Ateles*.

and Leighton (1994) who also proposed that brachiating primates have a greater choice of travel routes as well as being able to cross larger gaps than more quadrupedally adapted primates. Temerin and Cant (1983) and Cant (1986, p. 11) likewise have suggested that forelimb-dominated activities reduce pathway distances, increase speed of movement, and reduce energy expenditure—in particular, the “reduction of time expenditure during food harvest and travel.”

Is there a terrestrial quadrupedal phase before the advent of hominid bipedality?

Hand. Evidence from the hand has long been used to link hominoids (Keith, 1923, 1929; Gregory, 1928a,b; Clark, 1959; Napier, 1969, 1962; Tuttle, 1967, 1969a,b, 1970, 1972a,b; Washburn, 1968a; Lewis, 1969, 1971, 1972a–c, 1974, 1989; Marzke, 1971; Susman, 1979, 1983, 1988; Sarmiento, 1988; Marzke et al., 1994). The fine anatomical work of Lewis (1969, 1974) has prompted the greatest response in the literature concerning wrist function and ape evolution. Conroy and Fleagle (1972), Jenkins and Fleagle (1975), Tuttle (1967, 1969a,b, 1970, 1975), and Cartmill and Milton (1977) have provided alternative assessments of Lewis' interpretation of wrist function as reflecting a brachiating ape ancestry. However, the special nature of ape wrist anatomy has not been diminished within this debate; only the behavioral role for wrist function has been challenged.

In this debate, Lewis (1969, 1974) has argued persistently for a brachiating interpretation of hominoid wrist morphology, especially for the great apes. Conroy and Fleagle (1972) questioned Lewis' interpretation by simply asking why African apes, the most terrestrial of the living apes, would have a wrist anatomy better adapted for brachiation than do gibbons. Conroy and Fleagle (1972) further argued that the wrist anatomy of African apes is more likely associated with terrestrial quadrupedalism. Jenkins and Fleagle (1975) likewise noted several wrist features which distinguish African apes and *Macaca* from the Asian apes. Jenkins and Fleagle (1975, p. 225) stated in their comparison of the orientation of the triquetral and lunate articular surfaces that “In *Ma-*

caca, *Gorilla*, and *Pan* these surfaces are relatively broad and oriented in a proximal or proximo-ulnar direction. This arrangement appears more likely to be an adaptation for weight transmission and stability in extended, weight-bearing postures than for suspensory activity.”

Marzke (1971) also argued that the fused os centrale and limited abduction at the wrist in African apes and humans implied a terrestrial past within hominid evolution. Marzke (1971, p. 66) analyzed the fused os centrale, which is unfused in Asian apes, as an adaptation that serves “to strengthen the carpus in an important area of stress when weight is transmitted during knuckle-walking” in African apes, and therefore as a relict or ancestral character retained in humans. Recently, Marzke et al. (1994, p. 238) have suggested that one evolutionary scenario which could explain the type I lunatohamate and type III fourth carpometacarpal joints in *Australopithecus afarensis* is that the “Type III fourth carpometacarpal joint, with its strong resemblance to the chimpanzee pattern, could reflect knuckle-walking in *A. afarensis* or its ancestors.”

Sarmiento (1988, 1994) also examined wrist function in living apes and noted that African apes and humans share several quadrupedal weight-bearing features in the wrist. In particular, gorillas and humans share several additional features related to weight-bearing, including increased articular surfaces in the wrist, a further reduced ulnar styloid process, the absence of a separate and distinctive semilunar meniscus, and a large triangular articular disc (Sarmiento, 1988). “That humans share with gorillas many of the unique traits of the proximal carpal joint associated with quadrupedal terrestriality suggests a terrestrial quadrupedal ancestry for humans” (Sarmiento, 1988, p. 341).

The consensus of these works is that African apes and humans share a wrist anatomy that differs from that of the more arboreal orangutans or gibbons, and that the derived anatomical features of the African ape and human wrist support a functional interpretation of weight bearing during terrestrial quadrupedalism. African apes, of course, move this way daily but humans do not.

Thus, the only reasonable explanation for the presence of these features in the human wrist is that hominids shared a phase of terrestrial quadrupedalism with African apes prior to the advent of bipedality.

Foot. Foot anatomy has also linked hominoids (e.g., Gregory, 1916; Weidenreich, 1921, 1923; Morton, 1922, 1924a,b; 1935; Straus, 1930, 1949; Lamy 1983, 1986; Stern and Susman, 1983; Deloison, 1985; Latimer et al., 1987; Gebo, 1992a) and further supports the existence of a quadrupedal terrestrial phase prior to bipedality in human evolution. Gregory, as early as 1916, and later Weidenreich (1921) and Morton (1922) noted many similarities between the feet of gorillas and humans. In particular, the massiveness of the heel tuber, the flat talar body, the short talar neck, and the shorter and less curved phalanges and metatarsals of gorillas were likened to their human counterparts (Gregory, 1916; Weidenreich, 1921, 1923; Morton, 1922, 1924a,b, 1927, 1935; Keith, 1929). Gebo (1992a) also pointed out the unique role of heel-strike plantigrady in African apes and noted a variety of foot features and joint mechanics related to this footfall sequence and to terrestriality. Several of these features, such as the laterally rotated calcaneus, a dorsally elevated distal calcaneus with a broadened proximal heel region, an elevated navicular position with a large plantar ligamentous region, and the reorientation of the subtalar and transverse tarsal joints, also occur in hominids. Gebo (1992a, 1993) argued that the unique realignment of the tarsals due to heel-strike plantigrade footfalls is uniquely shared by African apes and humans and that hominid evolution most likely passed through a quadrupedal terrestrial phase.

Recently, Meldrum (1993) and Schmitt and Larson (1994, 1995) have questioned the notion the heel-strike plantigrady and the morphological features associated with it are unique evolutionary adaptations of African apes and humans, suggesting that orangutans also display the behavior described as heel-strike plantigrady. Further, since orangutans are arboreal and use heel-strike plantigrady, this suggests that heel-strike

plantigrady is not necessarily an adaptation for terrestriality.

As I outlined in my response to Meldrum (Gebo, 1993) and in the original study (Gebo, 1992a), orangutans are an interesting case to consider in terms of their behavioral and morphological associations with heel-strike plantigrady. Although orangutans do use heel-strike plantigrady when walking quadrupedally on the ground, the kinematic pattern of their footfalls is different from that of African apes (Schmitt and Larson, 1995). In addition, orangutans spend very small amounts of time on the ground (Rodman, 1984). The foot bones of orangutans are also very different from those of African apes and show no adaptations for heel-strike plantigrady. They have very long and curved toes, small tarsals relative to their large body size, and highly mobile joints (Tuttle, 1970; Langdon, 1984; Rose, 1988b). As noted by others, these foot features are related to the suspensory/climbing adapted movements most often utilized by orangutans (Tuttle, 1970; Langdon, 1984; Sarmiento, 1985; Rose, 1988b). The foot bones of orangutans do not have the reduced joint mobility or increased load-bearing features expected in a terrestrially adapted animal. Thus, heel-strike plantigrady in orangutans is unlike the behavioral-morphological complex found in African apes (Morton, 1924b; Gebo, 1992a).

There are two possible explanations for heel-strike plantigrady in orangutans. Heel-strike plantigrady may have been present in the ancestor of all great apes (Tuttle, 1975). This pattern of foot use is retained by orangutans, even though living orangutans are highly arboreal and have lost the anatomical features associated with heel-strike plantigrady. This view suggests that the ancestral great ape utilized terrestrial quadrupedalism, since heel-strike plantigrady is observed in orangutans when on the ground. See Smith and Pilbeam (1980) for a consideration of a terrestrial ancestral condition for orangutans.

There is some morphological evidence, although fragmentary, which supports a semi-terrestrial quadrupedal pattern of locomotion for *Sivapithecus*, a probable ancestor of orangutans (Pilbeam et al., 1980; Andrews and Cronin, 1982; Ward and Pilbeam, 1983),

akin to what we observe in chimpanzees today. The evidence of the two humeral shafts (GSP 30754 and 30730) and the distal humerus (GSP 12271) as well as the two calcanei (GSP 17152 and 17606) supports an interpretation of semiterrestrial quadrupedal locomotion for this extinct great ape. For example, the humeral shafts are strongly bowed medially as in terrestrial primates (see Gebo and Sargis, 1994), and they exhibit a retroflexed proximal shaft as in *Proconsul* and other more quadrupedally oriented primates (Pilbeam et al., 1990). Senut (1986) has further stated that the distal humerus of *Sivapithecus* is much more similar to African apes in its appearance and has interpreted these features to mean that *Sivapithecus* was partly terrestrial. Likewise, the two calcanei show subtalar and calcaneocuboid joint peculiarities that are unlike those of orangutans but are similar to foot features observed in the more terrestrial African apes (Gebo, 1992a). For example, the posterior part of the subtalar joint is broad and faces much more dorsally rather than being aligned proximodistally. This limits talar mobility along the calcaneus to subtle medial-lateral orientations (Rose, 1986) and is functionally related to greater load bearing, a subtalar feature characteristic of the more terrestrially oriented African apes (Gebo, 1992a). Further, the anterior part of the anterior subtalar facet is very wide and forms a long calcaneocuboid beak in *Sivapithecus* to help support the talar head, a condition also observed in African apes (Gebo, 1992a). Last, although the calcaneocuboid joint of both *Sivapithecus* and *Pongo* possesses a very deep pivot, there is extensive lipping along the lateral border of the calcaneocuboid joint in *Sivapithecus* (Rose, 1986). This lateral lipping limits the lateral rotation of the cuboid and acts as a bony stop during foot inversion. Thus, both the calcaneocuboid joint as well as the subtalar joint suggest limited mobility during foot inversion in *Sivapithecus*, the reverse of what we observe in *Pongo* where mobility for inversion is extremely well developed (Rose, 1988b). Further, the robust nature as well as the overall large size of the calcanei may also be indicative of increased use of the terrestrial substrate, especially when these features

are compared to *Pongo*. Although no heel region is preserved in these two calcanei, heel-strike plantigrady may well have been the norm for *Sivapithecus*, given the current morphological evidence. Thus, a terrestrial quadrupedal phase with heel-strike plantigrady for great apes is a distinct evolutionary possibility and this might help to explain the retention of heel-strike plantigrady in the specialized *Pongo*.

The alternative explanation suggests that the behavior and the morphological correlates of heel-strike plantigrady are shared uniquely by African apes and humans and that orangutans have independently evolved this behavior. The differences in the kinematics of heel strike between orangutans and African apes support this hypothesis. When orangutans come to the ground, having highly inverted feet adapted for arboreal suspension, they are "forced" to adopt a more lateral set of the foot compared to African apes, because of their long and curved toes. The heel does contact the ground in orangutans, but more on the lateral side of the foot. In fact, body support via the lower limb is often along the lateral side of the calcaneus, a very different situation from that of African apes. Thus, orangutan foot anatomy conforms as best as possible to terrestrial usage in a less than satisfactory manner. This is also in accord with the awkward hand postures that orangutans utilize when on the ground (Tuttle, 1969a, 1970). Similar postures are observed in tree sloths (Nowak and Paradiso, 1983), and the highly inverted foot postures of extinct ground sloths likewise forced foot contact along the lateral side of the calcaneus (Webb, 1989).

I prefer to view orangutans as having independently evolved heel-strike plantigrady in response to limited use of terrestrial quadrupedalism. This account explains the lack of morphological adaptations to heel-strike plantigrady in orangutans. The fossil record is still too incomplete and fragmentary for us to be confident of any other evolutionary assessment. However, the advent of heel-strike plantigrady is either at the node uniting the orangutan lineage and the African apes (Tuttle, 1975) or at the ancestral node for African apes and humans (Fig. 12; Gebo, 1992a). In either case, it seems most plausi-

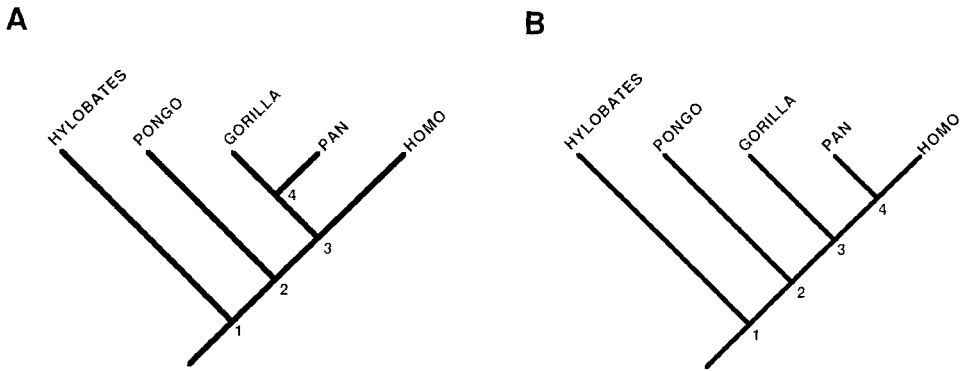


Fig. 12. **A,B.** Evolutionary relationships of apes and humans.

ble to relate heel-strike plantigrady with a terrestrial quadrupedal phase in great ape evolution.

Schmitt and Larson (1995) further believe that since *Ateles* during quadrupedalism places its heel in contact with an arboreal support after mid-foot contact, this animal should be categorized as "plantigrade." Since this "plantigrady" occurs in an arboreal setting, they contend that heel-strike plantigrady could have evolved within such a setting, eliminating any causal link with terrestriality. I disagree with this assessment for several reasons. First, primary mid-foot contact with subsequent heel touching of a support, in *Ateles* or in other primates (e.g., when standing or sitting), is a fundamentally different pattern of foot-support contact from heel-strike plantigrady, in which the heel contacts the support before the midfoot region does. Midfoot contact (what I have termed semiplantigrady) is in fact the foot-support posture used by almost all primates. Thus, secondary heel touching in *Ateles* or other primates is not fundamentally different from foot use in other arboreal or terrestrial primates that utilize mid-foot contact when moving quadrupedally. Therefore, great apes are very unusual in their footfalls compared to other primates, occasional heel touchers or not.

Further, it is difficult to conceive why a fully arboreal animal would evolve heel-strike plantigrady. In heel-strike plantigrady,

the heel contacts the substrate first. This puts the digits in an extremely disadvantageous position for grasping. In particular, climbing, especially vertical climbing, is not facilitated by the use of heel-strike plantigrady. In fact, heel-strike plantigrady is a foot position best used on top of a support. They only arboreal contact where grasping would be unimportant is on very large supports. Large supports, however, are quite rare. Large horizontal supports make up only 6% of the large- and medium-diameter branches of the ten most common trees at Kibale Forest (Gebo and Chapman, 1995). When arboreal, African apes use knuckle-walking and heel-strike plantigrady on large horizontal supports at rates of only 6.3% of all arboreal locomotion at Mahale (Hunt, 1992) or of 0.1% of bough use during quadrupedalism (Doran, 1992). Doran (1992, p. 93) notes that "As the diameter of a substrate decreases, the frequency of palmigrade quadrupedalism increases and that of knuckle-walking decreases." In the same way, heel-strike plantigrady should decrease as substrate diameters decrease. Heel-strike plantigrady is, however, always used when chimpanzees and gorillas are terrestrial. Orangutans also use heel-strike plantigrady when terrestrial, but use the largest arboreal supports (type 5 substrates) only 7% of the time during arboreal quadrupedalism (Cant, 1987). Since they rarely use the largest supports when arboreal (3% for all

arboreal locomotion; Cant, 1987), we can assume that heel-strike plantigrady is rare in the arboreal locomotion of orangutans, and is largely restricted to the terrestrial context.

Does early australopithecine limb anatomy support an "orangutanian phase" in human evolution, and, if so, how arboreal were early australopithecines?

Susman et al. (1985, p. 184) contend that the Hadar hominids practiced "a significant amount of climbing but that when they were on the ground they moved bipedally." This sounds very much like a modified chimpanzee in which terrestrial knuckle-walking has been replaced by terrestrial bipedalism, as opposed to an orangutan movement pattern. Stern and Susman (1983) and others (e.g., Senut, 1981; Tardieu, 1981; Tuttle, 1981; Jungers, 1982; Cook et al., 1983; Susman et al., 1984, 1985) have argued extensively for significant amounts of arboreality in *A. afarensis*. However, one must question the "arboreal features" present in early australopithecines as being representative of "intense" arboreality. In African apes, many "climbing" features are evident, but these are clearly primitive hominoid retentions. It is the heel-strike footfalls and the knuckle-walking adaptations of African apes that are innovative and evolutionarily derived. Yet, because African apes are alive today, we know that primitive features (e.g., long arms and curved fingers) function on a daily basis for climbing and feeding activities. On the other hand, we also know that the anatomy of the human wrist, elbow, and shoulder are related to an arboreal past that is not represented in the daily life of modern humans. How then are we to interpret primitive arboreal features found to occur in bipedal early australopithecines?

A. afarensis had already made a large anatomical commitment to bipedality, greater than that of any living ape (Stern and Susman, 1983; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990; Gebo, 1992a). If the Laetoli footprints belong to *A. afarensis* (Tuttle, 1985, 1990; Tuttle et al., 1991b) and if our interpretation concerning the hallux of *A. afarensis* (Latimer and Lovejoy, 1990) are

correct, it is clear that *A. afarensis* did not possess a grasping big toe (Lovejoy, 1978; Day and Wickens, 1980; Stern and Susman, 1983; White and Suwa, 1987; Latimer and Lovejoy, 1990; McHenry, 1991; Gebo, 1992a). Without a grasping big toe, it is hard to conceive of a hominid lower limb being well adapted for arboreality, moderately long and curved toes or not. Considering the evidence for the big toe and the decreased tarsal joint mobility compared to African apes (which are already largely terrestrial primates), it is unlikely that early australopithecine feet were utilized frequently in an arboreal context. It is more likely that the features of the early hominid lower limb, which are not exactly similar to modern humans and are thus more ape-like in appearance, represent features that are in evolutionary transition toward "advanced bipedality." This is likely the case for the new foot remains (Stw 573) from Sterkfontein (Clarke and Tobias, 1995) as well. The Stw 573 big toe is intermediate in its abducted span between that of chimpanzees and humans, and is exactly what one should expect to find in a transitional ancestral condition. The ability to abduct a big toe across an arc is not the same as a grasping toe, and thus the degree of arboreality or climbing capabilities interpreted for this specimen are suspect. Clarke and Tobias (1995) note that the proximal region of these four foot bones are very hominid-like, suggesting a severe reduction in tarsal mobility and loss of inversion capability, a key component for a grasping foot. These functional parameters severely limit the foot's ability to grasp or to climb effectively, thus questioning the degree of arboreality attributed to Stw 573 by Clarke and Tobias (1995). Although several individuals have interpreted Stw 573 as providing evidence for a strong arboreal component (see statements in Culotta, 1995), I would suggest that these foot elements help to document the evolutionary transition of deemphasis and eventual loss of a grasping big toe. Thus, the evidence for "intense arboreality" in the lower limb of early australopithecines appears rather doubtful. On the other hand, the more ape-like or primitive features that are found within the lower limb of *A. afarensis* argue for a somewhat less adept biped with shorter

strides and more muscular effort involved in striding relative to modern humans (Jungers, 1982; Stern and Susman, 1983; Reynolds, 1987). Jungers (1988) has likened australopithecine bipedalism to that of 6- to 13-year-old children in his citation of Foley et al. (1979). This assessment seems like a reasonable model for early australopithecine bipedalism.

The only relevant evidence for climbing and arboreality in *A. afarensis* comes from the interpretation of australopithecine forelimb anatomy. The hand and shoulder complex of *A. afarensis* shows several ape-like features (e.g., curved fingers, high glenoid angle, and long forelimbs), which are associated with arboreality, particularly "climbing" adaptations (Senut, 1981; Tuttle, 1981; Stern and Susman, 1983; Susman et al., 1984). Since these forelimb features are primitive ones, it is unclear as to what these forelimb features actually provide in terms of evidence for a "current use" understanding of early australopithecine locomotor/foraging behavior (see Szalay, 1981). I am sure that australopithecines could climb trees, just as modern humans occasionally do. But how much australopithecines utilized trees (to feed in, sit in, or sleep within) on a daily basis is a much harder question to answer. Given the primitive nature of the hominid forelimb, I see no resolution to this impasse.

PHYLETIC CONTEXT

In 1936, Adolph Schultz reviewed several alternative phylogenetic trees for humans and living apes. For example, Osborn (1930) and Clark (1934) viewed humans as being very early derivatives from the ape stock, whereas Schultz (1930), Keith (1931), and Gregory (1927b) envisioned a close relationship between humans and the great apes. On the other hand, Sonntag (1924), Smith (1924), and Weinert (1932) correctly believed that humans were more closely related to African apes, although each preferred a different taxonomic arrangement. Sonntag (1924) linked humans with both African apes, while Elliot Smith (1924) believed gorillas to be the sister taxon of humans. Only Weinert (1932) specifically linked chimpanzees with humans. Today, the genetic evi-

dence strongly favors a close evolutionary connection between African apes and hominids, although the debate continues concerning the exact relationships among chimpanzees, gorillas, and humans (e.g., Goodman et al., 1983, 1994; Sibley and Ahlquist, 1984; Miyamoto et al., 1987; Marks et al., 1988; Caccone and Powell, 1989; Sarich et al., 1989; Sibley et al., 1990; Rogers, 1993, 1994; Ruvolo et al., 1991; Ruvolo, 1994). Only two of the many historically proposed phylogenetic schemes are viable today, limiting the number of alternative explanations we can utilize to explain the morphological record and the locomotor changes in ape and human evolution.

Figure 12 illustrates the two most likely evolutionary phylogenies of hominoids. In both phylogeny A and B, I adopt Washburn's (1963) assumption that the unique upper body and forelimb anatomy of living apes evolved only once and place the features associated with this morphological complex at node 1. If this assumption is invalid—i.e., if hylobatids and great apes/humans have independently evolved these upper body and forelimb features—then these features would need to be placed separately onto nodes 1 and 2 for each phylogeny. At this time, I am unaware of any serious attempts to explain the upper body and forelimb morphological complex in great apes and hominids as representing independent evolutionary events, but the fossil arm evidence for *Sivapithecus*, *Kenyapithecus*, and "*Dryopithecus*" provide some evidence for such an idea (Pilbeam et al., 1990; Begun, 1992; McCrossin, 1994). If this should be the case (Simons, 1962, 1967; Napier, 1963), a very complicated sorting of convergent morphological features would be required. Likewise, if the upper body and forelimb morphological complex characteristic of living apes and humans evolved prior to the offshoot of hylobatids, then these features should be shifted to an earlier and more primitive node in each phylogeny. In any case, whether the upper body and forelimb morphological complex of living apes and hominids evolved once or several times, the evidence of the Atelini still suggests that a brachiating and forelimb-suspensory phase is a better explanation for

the upper body and arm anatomy of humans than is vertical climbing.

In phylogeny A, the African ape clade is a sister group to hominids (*Homo*), whereas in phylogeny B chimpanzees are the sister taxon of hominids (Fig. 12). If the protohominid went through an "orangutanian" phase (i.e., a climbing/suspensory ape which traveled arboreally) prior to assuming bipedality, as suggested by the vertical-climbing model, then node 3 in phylogeny A would have to represent an orangutanian-like ancestral condition for the African apes and hominids. This ancestral condition would represent a large-bodied, long-armed, very arboreal ape that is best likened to that of a female orangutan in terms of locomotor abilities. From this "orangutanian" ancestral condition, the knuckle-walking African apes and the bipedal hominids would emerge, and the hand features associated specifically with knuckle-walking, as well as any other adaptations that are uniquely shared by *Pan* and *Gorilla*, would evolve after node 3. Thus, features associated with weight-bearing and terrestriality (e.g., heel-strike plantigrady or a fused os centrale) would need to evolve twice, once in the African ape lineage, and once again in the hominid lineage. In phylogeny B, node 3 would represent the same "orangutanian" ancestral condition as in phylogeny A, but in this phylogeny the knuckle-walking and heel-strike adaptations of African apes need to have evolved separately in the chimpanzee and gorilla lineages. Again, as in phylogeny A, the terrestrial features associated with hominid bipedalism and terrestrial quadrupedalism in *Pan* would need to evolve independently. Given an "orangutanian" ancestral condition for protohominid ancestry, neither A nor B are parsimonious with respect to the terrestrial features shared by African apes and humans. Phylogeny B is even less parsimonious than phylogeny A.

On the other hand, if the ancestor at node 3 was a terrestrial quadruped, the weight-bearing features in the hand and foot that unite African apes and hominids can be interpreted as shared derived characters linking these two lineages, eliminating the need to interpret these features as evolutionary reversals. This change in the ances-

tral condition allows a more parsimonious character distribution in phylogeny A and still more so in phylogeny B. Further, the many anatomical features which have been used to distinguish each of the living hominoids in terms of locomotor function can also be widely accommodated within this evolutionary scenario. For example, Larson (1988) has documented differing degrees of humeral torsion within living apes and humans and has argued that quadrupedal apes, given their laterally positioned shoulder joints, must reorient their shoulders in the sagittal plane in quadrupedal locomotion. To accomplish this, higher torsional values are necessary and are observed in African apes (Larson, 1988). Larson believed that the high degree of humeral torsion in humans and African apes evolved independently, but noted that "It is also conceivable that this trait was inherited from a knuckle-walking ancestor shared with African apes" (p. 460). This latter view seems more probable (see also Begun, 1994) given the evidence of the hand and foot as well as the close molecular phylogenetic association of African apes and humans (Goodman et al., 1983; Sibley and Ahlquist, 1984; Miyamoto et al., 1987; Ruvolo et al., 1991; Rogers, 1993). Likewise, other anatomical differences in the elbow and wrist of living hominoids, as discussed by Tuttle (1967, 1975), Rose (1988a, 1993), and Sarmiento (1988) among others, can be explained as required morphological modifications for the movement patterns adopted by the great ape lineages after the brachiating/suspensory phase of hominoid evolution (Fig. 12, node 1). Any features shared by orangutans and hominids must either be primitive retentions or features shared in parallel (e.g., hip musculature, Stern, 1971).

Whether this quadrupedal terrestrial phase involved knuckle-walking is still a matter of contention. In the absence of any features associated with knuckle-walking in humans or early hominids, the knuckle-walking features of chimpanzees and gorillas could be placed at node 3 or node 4 of phylogeny A (Fig. 12). If, however, Phylogeny B is valid, a non-knuckle-walking ancestor of African apes and humans is unlikely. A knuckle-walking ancestor for hominids has been questioned on the basis of the lack of

knuckle-walking-associated features in hominids (e.g., Tuttle, 1967, 1969a,b; Stern, 1975; McHenry, 1984). However, there are reasonable explanations for this (see Shea and Inouye, 1993; Begun, 1994). First, no one has ever seriously suggested that australopithecines actively practiced knuckle-walking, so if these features are produced only by practicing knuckle-walking, there is no reason to expect their presence in hominids. In fact, why should we expect evidence of an antecedent phase to be present in a true descendant? Second, many features of the "knuckle-walking complex" are variably present or size-related in their expression in African apes (Sussman, 1979; Inouye, 1992; Shea and Inouye, 1993; Begun, 1994). Since many African apes knuckle-walk without these features, they are evidently not necessary for knuckle-walking (Shea and Inouye, 1993). Given the paucity of hominid hand bones and the small size of some early hominids, how likely are we to find these features? The hominid hand has also undergone a radical change in function since it no longer bears any weight during traveling locomotion. Since hominid digit function does not require any specialized weight-bearing features akin to those noted for African apes, the loss of these particular features might well be very rapid, especially if hominid hands were being modified to serve manipulative functions. Second, although the early hominids from Hadar are not "perfected" bipeds, they are well along the locomotor transition to bipedalism from a quadrupedal ape ancestry. Thus, we need to look earlier in time for transitional forms (approximately 5 to 7 mya) to document the presence and eventual loss of the hand features that are particular to African apes and to knuckle-walking.

SUMMARY

On balance, the evidence against a highly arboreal or an "orangutanian" phase immediately prior to hominid adaptation of bipedalism is growing. It is difficult to accommodate such a scenario given current interpretations of relationships among hominoids. Behavioral evidence indicates that all great apes, not just orangutans, engage

in significant amounts of vertical climbing, and thus chimpanzees and gorillas must also possess the necessary vertical-climbing preadaptations for the kinematics of human bipedalism. Shared features of the wrist in African apes and humans, features which are functionally related to stabilizing the wrist, support the idea of a terrestrial quadrupedal phase in hominid evolution. Such a hypothesis accords better with current interpretations of hominoid phylogeny. My alternative to the vertical-climbing model argues that early Miocene hominoids like *Proconsul* were arboreal, quadrupedal, and quite capable of vertical climbing/clambering. Later, hominoid bodies underwent a radical morphological shift representing the ancestral condition for gibbons, great apes, and humans. Slow to moderate-speed brachiation, orthograde body postures, and uni- or bimanual suspension feeding evolved, and this complex was more than likely a single adaptive event resulting in the unique features of the extant hominoid thorax and forelimb.

Choosing between 1) the evolution of large body size as the next phase in hominoid evolution as in Keith's view or 2) large body size representing the ancestral condition of living apes, is difficult. Both have several evolutionary implications. If large body size represents the primitive condition for living apes, then gibbons have reduced in size and become quite active ricochet brachiators. If small body size is primitive for living apes, then the common ancestor of orangutans and the African apes increased in size, with the orangutan lineage adapting to complex, high canopy pathways by using versatile climbing and their already present suspensory abilities (see Tuttle, 1975). With large size also comes an increase in quadrupedalism and an increase in vertical climbing frequencies from that of gibbons. Travel was largely arboreal. The ancestors of the African apes continued to move using quadrupedalism and climbing, but began to use the terrestrial substrate for travel, adopting quadrupedal postures. It is here that ancestral African apes developed a foot morphology associated with heel-strike plantigrade footfalls, a weight-bearing wrist, and perhaps knuckle-walking fingers as functional-adaptive com-

plexes for terrestrial quadrupedal travel. Since African apes represent the closest living relatives of hominids, it would seem best to ascribe a long history of such terrestriality to the ancestral protohominid. Thus, the best explanation for the evolutionary locomotor transition toward hominid bipedalism is through a terrestrial and quadrupedal phase like that of the African apes (Washburn, 1968a,b, 1971; Marzke, 1971; Sarmiento, 1988; Gebo, 1992a). Although this ancestor would still be quite capable as a climber, as are African apes today, climbing and the morphological associations with it represent only primitive hominoid adaptations. In fact, vertical climbing with a brachiating type of body plan can still be functionally preadaptive for hominid bipedalism; but this alone cannot explain the weight-bearing adaptations retained in the hands and feet of hominids. I believe hominid bipedalism simply continues the terrestrial traveling trend evident in African apes, but allows hominids to free their hands from the burden of support. Thus, carrying becomes one of the key ecological innovations of protohominids prior to the advent of efficient bipedalism (Hewes, 1961; Lovejoy, 1981). If we truly accept either of the two phylogenies outlined in Figure 12, I believe that the behavioral, anatomical, and historical record offers little support for a highly arboreal phase immediately prior to the rise of hominid bipedalism. It seems much more likely that a quadrupedal terrestrial phase is essential for the development of human bipedalism.

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